Tree Physiology 24, 775–784

Physiological, morphological and allocational plasticity in understory deciduous trees: importance of plant size and light availability

SYLVAIN DELAGRANGE,[1,2] CHRISTIAN MESSIER,[1,3] MARTIN J. LECHOWICZ [4] and PIERRE DIZENGREMEL[2]

[1] *Groupe de Recherche en Ecologie Forestière inter-universitaire (GREFi), Université du Québec à Montréal, C.P. 8888, Succ. Centre ville, Montréal, Québec, H3P 3P8, Canada*

[2] *Ecophysiologie cellulaire et moléculaire UMR 1137 INRA - UHP Nancy Ecologie et écophysiologie forestières BP 239, 54506 Vandoeuvre, France*

[3] *Corresponding author (messier.christian@uqam.ca)*

[4] *Department of Biology, McGill University, 1205 Avenue Dr. Penfield, Montréal, Québec, H3A 1B1, Canada*

Received August 11, 2003; accepted December 21, 2003; published online May 3, 2004

Summary In a 4-year study, we investigated changes in leaf physiology, crown morphology and whole-tree biomass allocation in seedlings and saplings of shade-tolerant sugar maple (*Acer saccharum* Marsh.) and intermediate shade-tolerant yellow birch (*Betula alleghaniensis* Britt.) growing in natural understory light (0.5 to 35% of full sunlight) or in understory light reduced by 50% with shade nets to simulate the effect of gap closure. Leaf physiological parameters were mainly influenced by the light gradient, whereas crown morphological and whole-tree allocational parameters were mainly influenced by tree size. No single physiological, morphological or allocational trait was identified that could explain the difference in shade tolerance between the species. Yellow birch had higher growth rates, biomass allocation to branches and leaf physiological plasticity and lower crown morphological plasticity in unmodified understory light than sugar maple. Sugar maple did not display significant physiological plasticity, but showed variation with tree size in both crown morphology and whole-tree biomass allocation. When sugar maple was small, a greater proportion of whole-tree biomass was allocated to roots. However, physiological differences between the species decreased with decreasing light and most morphological and allocational differences tended to disappear with increasing tree size, suggesting that many species differences in shade-tolerance are expressed mainly during the seedling stage. Understory trees of both species survived for 4 years under shade nets, possibly because of higher plasticity when small and the use of stored reserves when taller.

Keywords: Acer saccharum, Betula alleghaniensis, biomass partitioning, carbon assimilation, carbon balance, crown morphology, shading, sugar maple, tree height, yellow birch.

Introduction

Solar irradiance is usually low and highly variable in the understory of temperate deciduous forest (Runkle 1982, Canham et al. 1990, Beaudet et al. 2000). Because light is often the most limiting resource for growth of understory seedlings and saplings (Bellefleur and LaRocque 1983*b*, Ricard et al. 2003), light availability in the understory is frequently associated with regeneration processes and the long-term survival of forest tree species (McClure et al. 2000, Woods 2000). The growth and survival of understory trees is closely dependent on their ability both to acclimate to sudden increases in irradiance caused by a break in the canopy and to tolerate low irradiances for lengthy periods until a canopy gap occurs. Such abilities are species dependent (Baker 1949, Forcier 1975) and result from: (a) variation in the combination of numerous traits; and (b) differing degrees of trait plasticity related to environmental modifications (Givnish 1988, Tilman 1988, Gleeson and Tilman 1992).

In response to continual spatio-temporal changes in the light environment, trees modify their leaf physiology, crown morphology and whole-tree biomass allocation (Beaudet and Messier 1998, Gardiner and Hodges 1998, Canham et al. 1999, Walters and Reich 1999). However, many characteristics of understory trees vary with tree size (King 1986, Bond 2000, Naumburg et al. 2001, Sterck and Bongers 2001, Claveau et al. 2002) in ways that can impact the shade tolerance of species (Givnish 1988, Messier et al. 1999, Messier and Nikinmaa 2000). Thus, to better understand mechanisms involved in understory tree regeneration, integrated studies of numerous tree traits in relation to light, plant size and their interaction are needed.

In this study, we investigated how leaf physiology, crown morphology and whole-tree biomass partitioning vary along both light and size gradients in two temperate deciduous tree species: yellow birch (*Betula alleghaniensis* Britt.) and sugar maple (*Acer saccharum* Marsh.). Sugar maple, a late-successional species, is extremely shade tolerant (Baker 1949, Godman et al. 1990), although it is relatively fast growing in the open (Canham 1988). Yellow birch, which exhibits intermediate shade tolerance, is a mid-successional species (Baker

1949, Erdmann 1990) that shows rapid growth in open conditions (Bellefleur and LaRocque 1983*a*, Beaudet and Messier 1998). Despite contrasting functional ecology and successional status, yellow birch and sugar maple co-occur in eastern North America.

We studied regenerating seedlings and saplings of both species growing in both natural understory light and in understory light reduced by 50% with shade nets to simulate gap closure. Our main objectives were to examine variation in the physiological and morphological traits of understory sugar maple and yellow birch in relation to light availability and tree size, and to assess the adaptive significance of this variation.

Materials and methods

Study site

This study was carried out in the Duchesnay experimental forest (46°55′ N, 71°40′ W) near Québec City, Canada. Site elevation ranges from 200 to 300 m, annual rainfall is around 1220 mm and mean daily temperature ranges from 28 °C in July to –12 °C in January. The soil is a ferro-humic podzol with a thin humus layer over a more or less well-drained glacial till. The forest canopy is mainly dominated by sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britt.) and American beech (*Fagus grandifolia* Ehrh.). American yew (*Taxus canadensis* Marsh.), striped maple (*Acer pennsylvanicum* Lam.) and moosewood (*Viburnum alnifolium* Marsh.) predominate in the understory. Dominant trees of the experimental forest were around 90 years old and 22 m tall. Total stand basal area was 27 m^2 ha^{-1} (596 stems per hectare). Mean tree diameter at breast height (DBH) was 26 cm, but 61% of living stems had a DBH of < 20 cm.

Shading treatment and light measurements

We sampled two stands in close proximity. One stand had been selectively cut in 1989 and the other in 1994, allowing us to find naturally regenerated seedlings and saplings of different sizes over a wide gradient of light conditions (Table 1). To simulate the rapid closing of a canopy gap, 32 shade nets were installed in gaps of each stand during spring 1997. Nets were removed during winter and reinstalled each spring at least 1 m above the understory vegetation. One-meter net curtain walls were sewn to the main horizontal net to reduce lateral irradiance.

Light availablility was quantified on four overcast days during July 2000 (Messier and Puttonen 1995) by taking three instantaneous light measurements at 5 cm above the top of the seedlings with an LI-189 radiometer (Li-Cor, Lincoln, NE). At the same time, in an adjacent area, a quantum sensor linked to a Li-Cor LI-1000 data logger measured light every 5 s and recorded the mean every minute. To calculate the percentage of total overstory light available, the values recorded above the trees were divided by the reference value taken at the same time in the open area. Instantaneous light measurements taken in overcast conditions are highly correlated to the mean seasonal daily light percentage (Gendron et al. 1998). Available light measured at the top of unshaded understory trees in year 2000 varied from 0.5 to 35% of full sunlight, whereas light ranged from 0.5 to 16% of full sunlight above the artificially shaded understory trees.

Tree measurements and harvesting

During summer 2000, 46 sugar maple and 44 yellow birch were studied and then harvested. Leaf maximal carbon dioxide (CO_2) assimilation (A_{max}; μmol CO_2 m^{-2} s^{-1}), leaf maximal stomatal conductance (g_{smax}; μmol CO_2 m^{-2} s^{-1}) and leaf dark respiration (R_d; μmol CO_2 m^{-2} s^{-1}) were measured between July 10 and 27 with a Li-Cor LI-6400 gas exchange analyzer. For A_{max}, R_d and g_{smax} measurements, one leaf per tree was chosen from the upper crown layer. Light was maintained at 1500 and 0 μmol m^{-2} s^{-1} during the A_{max} and R_d measurements, respectively, leaf temperature was set at 25 °C, air CO_2 concentration at 375 μmol CO_2 mol^{-1} and relative humidity was maintained between 60 and 75%. Measurements of A_{max} were recorded after an activation period of at least 10 min. Leaf dark respiration measurements were taken after 5 min of darkness when gas exchanges reached a steady state. Measured leaves were then harvested and dried at 65 °C for 48 h and used to estimate area-based leaf nitrogen concentration (N_a; g m^{-2}) with an elemental NCS 2500 analyzer (ThermoQuest, Milan, Italy).

At the end of August 2000, both above- and belowground parts of all the experimental trees were harvested and several biomass partitioning and morphological traits were measured. To collect total coarse and fine root biomass of each tree, each root was excavated by hand. Main stem length, height of the crown base (i.e., height to the first live branch) and stem diameter at the ground-line were measured. From the height of the crown base and the mean of two perpendicular crown diameters, we calculated: (a) the crown height over crown diameter ratio (Crown H/D); (b) percent of live crown relative to total tree height (%Crown); and (c) number of first-order living

Table 1. Description of harvested seedlings and saplings sampled in summer 2000 in two selection cuts in close proximity at the Duchesnay experimental forest station in Québec, Canada. Values for height and age are means ± SE.

	Old cut (1989)		Young cut (1994)	
	Sugar maple	Yellow birch	Sugar maple	Yellow birch
No. of harvested trees	23	20	23	24
Tree height (cm)	175.50 (± 18.73)	269.22 (± 27.39)	54.02 (± 5.73)	102.62 (± 10.15)
Tree age (years)	13.87 (± 0.77)	10.55 (± 0.52)	9.09 (± 0.53)	5.17 (± 0.17)

branches per 10 cm of crown length. Roots (fine: < 2 mm, coarse: > 2 mm), stem, branches and leaves were then separated, dried at 65 °C for 48 h, and weighed to calculate the fine root mass ratio (FRMR; fine root to total tree dry mass (DM)), the percentage of leaf or photosynthetic tissue (PT), branch, stem and total root percentage in total tree DM and the ratio of non-photosynthetic (NPT) to photosynthetic tissue. Two to six 7-cm^2 leaf disks (depending on crown size) were randomly taken within the crown and dried to obtain leaf mass area (LMA; g m^2). Total leaf area for each tree was calculated from LMA and total foliar dry mass (DM), excluding petioles. We then calculated leaf area as a ratio of total plant dry mass (LAR; m^2 g^{-1} plant). Annual height growth for the last 2 years was determined by measuring from the shoot apex to the bud scales of the penultimate year's shoot, and radial growth was estimated by growth ring analysis of the bisector of the smallest and largest radius of a sanded stem section. Radial increment measurements were made with a Quick Chek measuring unit (QC1000, Metronics, Bedford, NH) coupled to a computer program (MeasureJ2X, V3.1, VoorTech Consulting, Holderness, NH). Relative height and radial growth (RHG and RRG) were calculated from the height and radial growth measurements as:

$$\text{RHG of year } n = \frac{(\text{Height}_n - \text{Height}_{n-1})}{\text{Height}_n} \quad (1)$$

$$\text{RRG of year } n = \frac{(\text{Radial}_n - \text{Radial}_{n-1})}{\text{Radial}_n} \quad (2)$$

Data analysis

All statistical analyses were performed with SAS Version 8.02 (SAS Institute, Cary, NC). The effects of tree size and of light gradient on various traits of both species were examined in unshaded seedlings and saplings in natural understory light. Variation in each trait against gradients of light percentage and tree size were evaluated by analysis of covariance (ANCOVA), where species was a factor and light percentage and tree size were co-variables. Data transformations were made on co-variables (size and light) when necessary to reach residue normality and variance homogeneity needed for the analyses.

To evaluate species responses to the artificial attenuation of understory light, we compared trees of two size groups (short and tall) found under shade nets with trees of comparable size that were not shaded by the nets. To define traits that distinguished short and tall plants under natural and shaded conditions, we performed a canonical discriminant analysis (CANDISC procedure in SAS) with the distance ANOVA option that uses the Mahalanobis distance parameter to determine statistical differences between the mean vector of each group. The 87 trees in the analysis were separated into eight groups (Table 2). Coding for each group was defined by treatment (Sh = shaded and USh = unshaded), size of our populations (S = small and T = tall, cf., Table 1) and species (M = sugar maple and B = yellow birch). Traits included were A_{max}, %PT, %Branch, %Root, Crown H/D and number of branches per unit crown length (dm). Traits were chosen for statistical independence from one another.

Results

Effects of light and size gradients

Tree growth Relative height growth (RHG) was significantly influenced by light availability in both species, whereas relative radial growth (RRG) depended on both tree size and species (see Growth in Table 3). Yellow birch showed greater height and radial growth than sugar maple over the entire range of the light and size gradients, but differences were not significant (data not shown).

Leaf physiology Light was a significant factor affecting g_{smax}, whereas size and species alone were not (Table 3). A similar pattern was observed for A_{max} (Figure 1B), whereas light was the only significant factor affecting R_d. In both species, A_{max} was correlated with g_{smax} ($A_{max} = 0.0374 g_{smax} + 5.6026$; $r^2 = 0.54$ for yellow birch and $A_{max} = 0.0574 g_{smax} + 4.389$; $r^2 = 0.50$ for sugar maple, data not shown). Light availability, tree size and species each had a significant or near significant effect on N_a (Table 3, Figure 1D). With increasing light availability, yellow birch had increasingly higher g_{smax} and A_{max} than sugar maple (Figures 1A and 1B), whereas N_a was higher in yellow birch than in sugar maple at all irradiances. None of the mea-

Table 2. Summary of the experimental design for the eight groups used in the canonical discriminant analysis to evaluate the effect of a sudden imposed shading (Sh) compared with an unshaded treatment (USh) in two contrasting populations (T = tall and S = small) of sugar maple (M) and yellow birch (B).

Selection cuts (cf. Table 1)	Treatment	Species	*n*	Code	Individual growth history after cutting
Old cut (taller trees)	Sh	M	11	ShTM	At least 6 years USh then 4 years Sh
		B	11	ShTB	At least 6 years USh then 4 years Sh
	USh	M	11	UShTM	At least 10 years USh
		B	10	UShTB	At least 10 years USh
Young cut (smaller trees)	Sh	M	12	ShSM	At least 1 years USh then 4 years Sh
		B	12	ShSB	At least 1 years USh then 4 years Sh
	USh	M	11	UShSM	At least 5 years USh
		B	9	UShSB	At least 5 years USh

Table 3. Summary of ANCOVA *P* values (* indicates significant values at $\alpha = 5\%$) for relationships between growth, physiological, morphological and allocational parameters and species (SP), tree size (S), light (L) and the interactions of SP, S and L. Abbreviations: relative height growth (RHG); relative radial growth (RRG); maximal stomatal conductance (g_{smax}; μmol m^{-2} s^{-1}); maximal CO_2 assimilation rate (A_{max}; μmol CO_2 m^{-2} s^{-1}); leaf dark respiration (R_d; μmol CO_2 m^{-2} s^{-1}); leaf nitrogen amount (N_a; g m^{-2}); percentage of total tree dry mass in photosynthetic tissues (%PT), non-photosynthetic tissue (%NPT), branch (%Branch), stem (%Stem) and root (%Root); leaf area ratio (LAR; cm^2 g^{-1} plant); fine root to whole plant mass ratio (FRMR); percent of live crown in total tree height (%Crown); crown height over diameter (Crown H/D); and number of lateral meristems per 10 cm of crown length (Branches per CL).

Parameter	SP	S	L	SP × S	SP × L	S × L	SP × S × L
Growth							
RHG	0.0577	0.2198	0.0082 *	0.4810	0.4906	0.1987	0.4619
RRG	0.0106 *	0.0049 *	0.1523	0.6415	0.2207	0.1387	0.2104
Physiology							
g_{smax}	0.5108	0.5285	< 0.0001 *	0.3427	0.0003 *	0.2691	0.0970
A_{max}	0.8671	0.3853	< 0.0001 *	0.0884	0.0066 *	0.8876	0.0843
R_d	0.5401	0.2926	0.0497 *	0.7437	0.4940	0.6001	0.8211
N_a	0.0137 *	0.0679	0.0141 *	0.5677	0.4727	0.2348	0.7664
Allocation							
%PT or %NPT	0.1703	0.0096 *	0.2769	0.1760	0.0663	0.3358	0.0825
%Branch	0.0001 *	< 0.0001 *	0.1359	0.0041 *	0.0181 *	0.5364	0.0870
%Stem	0.8972	0.0094 *	0.4335	0.3713	0.7067	0.7449	0.9335
%Root	0.0380 *	0.0006 *	0.4465	0.0132 *	0.2032	0.2482	0.0659
LAR	0.5481	0.0047 *	0.7357	0.4407	0.1838	0.9069	0.1940
FRMR	0.1000	< 0.0001 *	0.3240	0.1118	0.0881	0.3431	0.0944
Morphology							
%Crown	0.0108 *	0.0089 *	0.0143 *	0.0295 *	0.3741	0.0061 *	0.0695
Crown H/D	0.0100 *	0.0683	0.1322	0.0483 *	0.8848	0.3230	0.1792
Branches per CL	0.0041 *	0.0336 *	0.2424	0.0163 *	0.1018	0.3551	0.1499

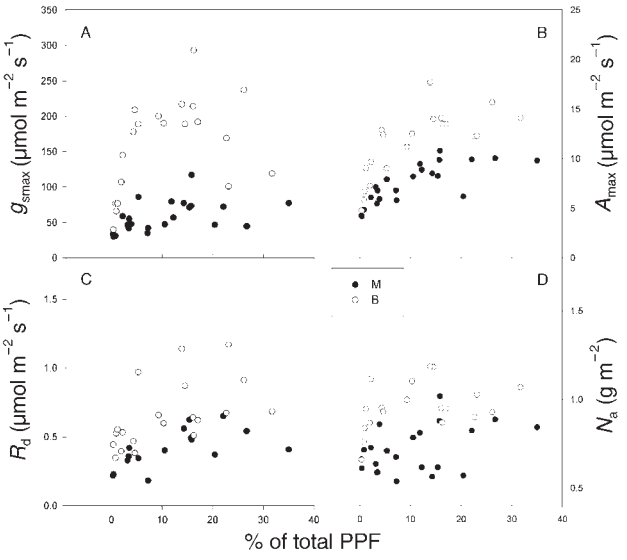

Figure 1. Leaf physiological parameters versus % of total photosynthetic photon flux (PPF) for sugar maple (M; ●) and yellow birch (B; ○) seedlings and saplings measured in the Duchesnay forest station, Québec, Canada. Abbreviations: g_{smax} = maximal stomatal conductance; A_{max} = maximal CO_2 assimilation rate; R_d = leaf dark respiration; and N_a = area-based leaf nitrogen concentration.

sured leaf physiological parameters varied with tree size (Table 3).

Biomass partitioning Tree size was the main factor associated with variations in biomass partitioning, whereas light had no effect except for an interaction between species and light for %Branch (Table 3). Although %PT significantly decreased with increasing tree size (Figure 2), the effects of light availability and species were not significant (Table 3). With increasing tree size, %Branch increased significantly, and there were significant interactions between tree size and species, and between light and species, indicating that yellow birch tended to allocate more biomass to branches than sugar maple, and that this difference tended to disappear as the trees get larger or as light availability increases (data not shown). Although %Stem significantly increased with tree size, there was no significant interaction with species or light. The value of %Root tended to decrease with tree size (see Allocation in Table 3), and the significant interaction between species and tree size suggests that this decline was greater for sugar maple than for yellow birch (data not shown).

Leaf area ratio did not differ between species, but it decreased rapidly with increasing tree size (Table 3). A similar pattern was observed for FRMR, which decreased with in-

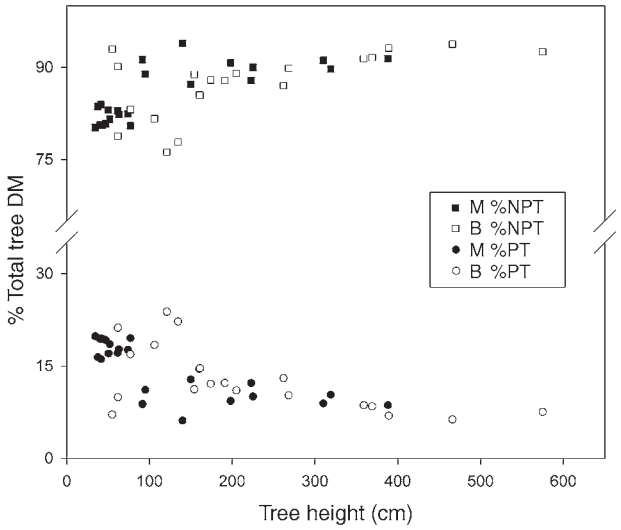

Figure 2. Effect of tree height on the proportion of non-photosynthetic tissues (NPT; ■ and □) and photosynthetic tissues (PT; ○ and ●) in total tree dry mass (DM) of sugar maple (M; ■ and ●) and yellow birch (B; □ and ○) seedlings and saplings measured in the Duchesnay forest station, Québec, Canada.

creasing tree size (Figures 3A and 3B), but was unaffected by light availability or species (see Allocation in Table 3).

Crown morphology All variables tested significantly affected %Crown, and there were significant interactions between light and tree size and between species and tree size (see Morphology in Table 3). The value of %Crown was mainly influenced by light when plants were small with the result that differences between species decreased with increasing size. Overall, yellow birch showed a greater %Crown (data not shown), a greater Crown H/D (Figure 4A) and a greater number of branches per unit of crown length than sugar maple (Figure 4B). However, the significant interaction between plant size and species for these parameters indicated a decrease in species differences with increasing tree size. Variation in Crown H/D was influenced less by tree size in yellow birch than in sugar maple (Figure 4A). The number of branches per unit of crown length differed between species (Figure 4B). Yellow birch had many branches but a declining number per unit crown length with increasing tree size, whereas sugar maple showed a highly variable ratio when small but a more stable ratio with increasing tree size. Most sugar maple seedlings had fewer branches than yellow birch seedlings; however, when saplings were more than 1 m tall, sugar maple had a similar number of branches per unit of crown length as yellow birch.

Effect of artificial shading

Canonical discriminant analysis showed significant discrimination among the eight groups along three canonical axes. The first axis (CAN1) explained 76% of the variation (Eigenvalue = 4.23, $F = 5.43$, $P < 0.001$) and the second axis explained 14% (Eigenvalue = 0.78, $F = 2.50$, $P < 0.0001$), whereas the third axis explained only 8% and was at the limit of significance (Eigenvalue = 0.48, $F = 1.58$, $P = 0.041$). Consequently, the results presented in Figure 5 show only the discrimination on the first two axes. The first axis mainly discriminated among groups based on differences in allocational traits (see parameter vectors in Figure 6) such as %Root and %PT versus %Branch. The first axis also separated groups based on Tree H/D and A_{max}. In Figure 6, CAN2 discriminated groups based mainly on contrasting A_{max}, %Root, N_a and Crown H/D, and CAN3 separated groups based on differences in A_{max} and %PT (vectors not shown).

Yellow birch had consistently higher N_a, A_{max}, %Branch and Tree H/D, but lower %Root than sugar maple (Table 4, Figures 5A and 5C versus 5B and 5D), and there was a clear separation between short and tall trees. In both species, shorter saplings had higher A_{max}, %Root and %PT, whereas taller saplings had higher N_a, %Branch and Crown H/D (Table 4, Figures 5A and 5B versus 5C and 5D).

Although the shading treatment had no impact on individual mortality, it significantly affected leaf physiology, crown morphology and whole-tree biomass partitioning in both species and plant height groups (except for taller sugar maples where

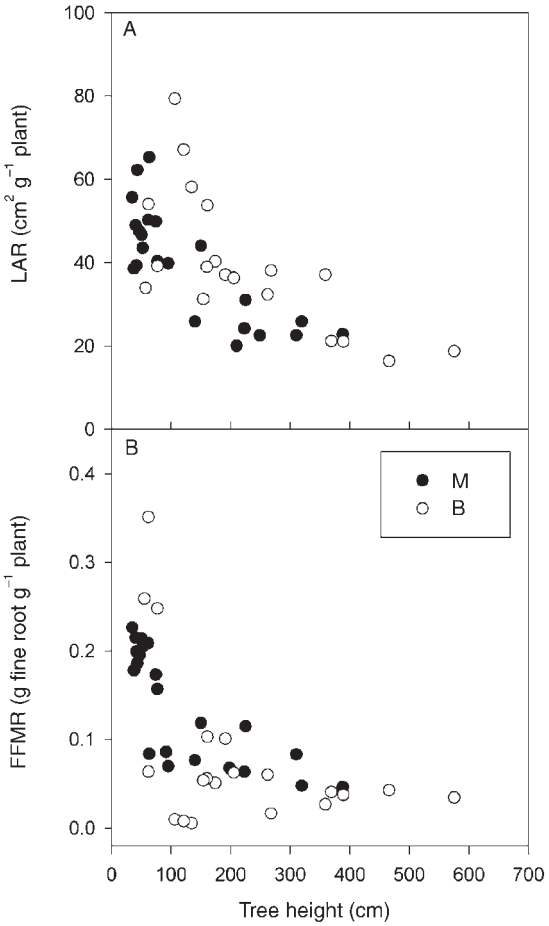

Figure 3. Variations in whole-tree allocational parameters versus tree height in sugar maple (M; ●) and yellow birch (B; ○) seedlings and saplings measured in the Duchesnay forest station, Québec, Canada. Abbreviations: LAR = leaf area ratio; and FRMR = fine root mass ratio.

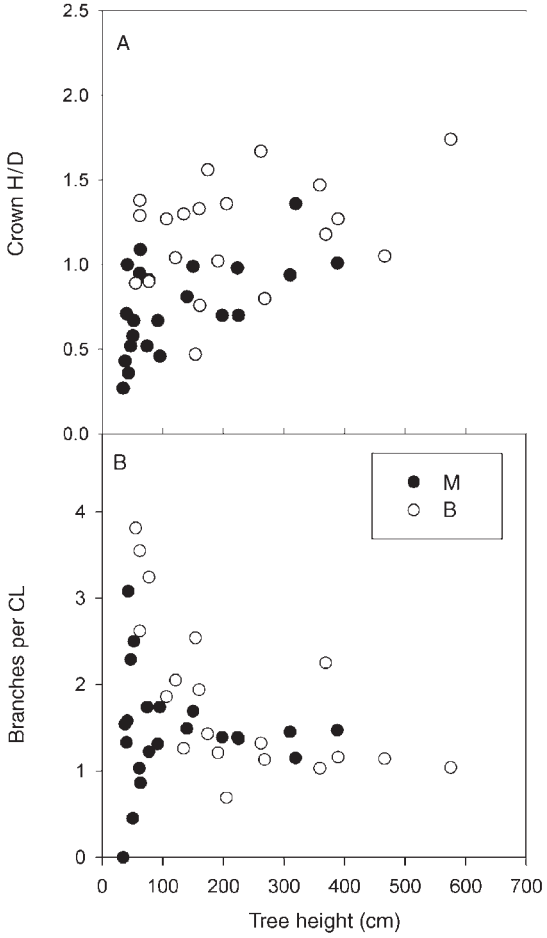

Figure 4. Variations in crown morphological parameters versus tree height in sugar maple (M; ●) and yellow birch (B; ○) seedlings and saplings measured in the Duchesnay forest station, Québec, Canada. (A) crown shape (crown height over crown diameter ratio (Crown H/D)), and (B) number of branches per 10 cm of crown length (Branches per CL).

the difference was not significant (P = 0.8376; Table 4, Figure 5C)). Differences between shaded and unshaded groups were greater for yellow birch than for sugar maple (Table 4). Crown H/D, N_a, and %Branch were lower in shaded yellow birch than in unshaded yellow birch (Figures 5B and 5D). Although shading had no significant impact on taller sugar maples, it resulted in a reduction in A_{max}, %PT and %Root in shorter seedlings (Figure 5). In both species, shading caused small reductions in A_{max} and %PT along CAN3 (data not shown). However, shading dramatically increased the NPT/PT ratio for several shorter trees belonging to the ShSM and ShSB groups (Figure 7). These seedlings were subject to some kind of stress as indicated by the small number of leaves and the presence of yellow leaves and dead branches.

Discussion

Plasticity along light and size gradients

Variation in light availability was mainly responsible for variations in leaf physiological traits, especially in the moderately shade-tolerant yellow birch (Figure 1). The strong and direct effect of light on photosynthetic capacity was mainly related to light-induced variations in the pool of proteins, pigments and enzymes (i.e., N_a) that supports light capture and CO_2 fixation by leaves (Niinemets et al. 1998, Le Roux et al. 1999). Increased A_{max} with increasing light was also associated with increased stomatal conductance. Higher g_{smax} enhances CO_2 diffusion into leaves, which in turn increases photosynthetic rates. However, although increased light availability is associated with greater stomatal conductance (Jarvis 1976, Le Roux et al. 1999), stomatal regulation mechanisms remain poorly understood. The variations in g_{smax} observed here (Figure 1A, Table 2) may be more dependent on stomatal density and size than on other factors.

Variation in light availability also induced variations in CO_2 losses because of variations in leaf respiration (R_d in Figure 1C, Table 3). Higher irradiances probably increased R_d as a result of higher maintenance costs caused by higher photosynthetic rates (Amthor 1986, Niinemets et al. 1998), higher protein turnover and increased need for secondary compounds such as flavonoids or carotenoids. The increased R_d observed for yellow birch is also likely related to its continuous growth (cf. Amthor 1986) compared with sugar maple.

We found that traits associated with the partitioning of tree biomass were mainly dependent on tree size as has also been reported for diverse annual plant species by McConnaughay and Coleman (1999). In agreement with data for evergreen conifers (Claveau et al. 2002), we found that the NPT/PT ratio increased with tree size. Here NPT also included belowground parts, which have rarely been quantified for such large saplings growing in natural conditions. The increase in the proportion of NPT in total tree dry mass (Table 3) is the direct consequence of the annual addition of new branches, roots and trunk rings that support tree foliage (Givnish 1995). Based on the pipe model theory (cf. Perttunen et al. 1998), every increase in leaf area exponentially increases the surface area needed for water transport and will increase the volume of NPT. This increasing investment in woody tissues is imposed by the need to maintain mechanical strength to cope with the increasing stress caused by wind and gravity as tree size increases (King 1986, Niklas 1992).

According to the hypothesis of Givnish (1988), increases in NPT/PT ratio with increasing tree size will negatively affect tree carbon balance. Although this hypothesis may hold true for smaller seedlings as long as all their NPT is actively respiring, it is questionable whether increases in NPT/PT ratio negatively impact the carbon balance of taller trees. Taller trees annually reduce active NPT dry mass by producing inactive heartwood (Ceschia 2001), which reduces the respiratory cost of the trunk without reducing physical support. Taller trees may also benefit from an increase in NPT/PT ratio by improving their hydraulic conductance (Ryan et al. 2000, McDowell et al. 2002) and increasing the amount of carbohydrate storing tissue. Nevertheless, to test the overall effects of increasing tree size on tree functions, accurate estimates of daily and seasonal individual carbon balance under contrasting light environments and at different developmental stages (based on individual tree growth models) are needed.

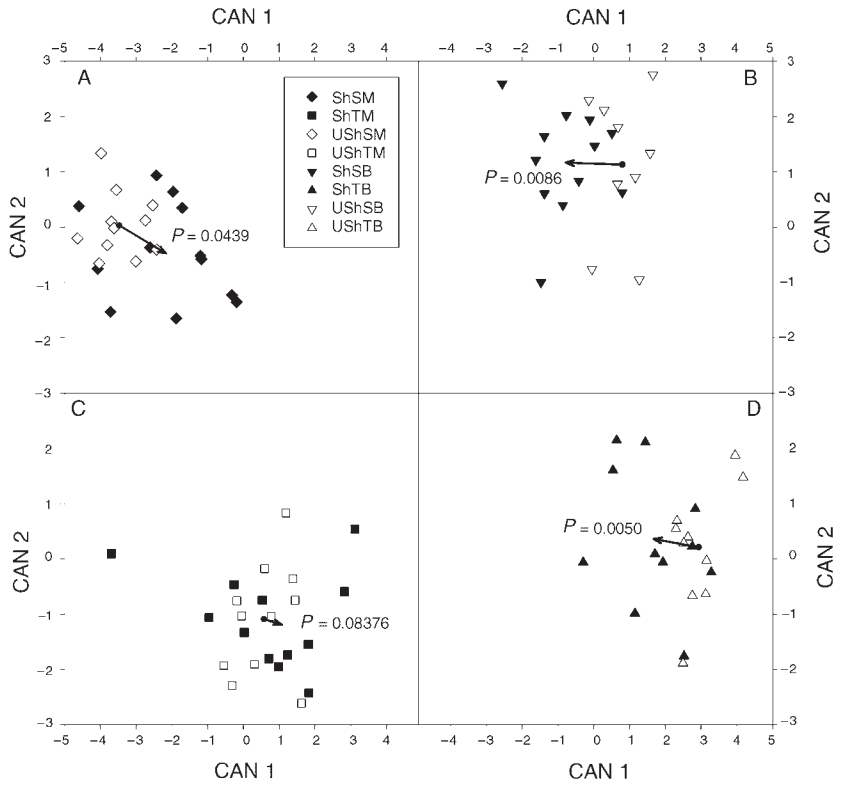

Figure 5. Graphical representation of the canonical discriminant analysis results for shaded (Sh) (solid symbols) and unshaded (USh) (open symbols) sugar maple (M) and yellow birch (B) divided into two size groups, short (S) and tall (T). Shown are the two main axes that cumulatively accounted for 90% of the total variation. (A) Short sugar maple groups (◆ and ◇). (B) Short yellow birch groups (▼ and ▽). (C) Tall sugar maple groups (■ and □). (D) Tall yellow birch groups (▲ and △). Vectors from the mean of unshaded groups to the mean of shaded groups as well as probability of the means of the two groups being significantly different at $\alpha = 5\%$ are indicated.

Our results are in agreement with other studies showing that crown morphology is influenced not only by light availability, but also by plant size and species (Poorter and Werger 1999, Naumburg et al. 2001, Sterck and Bongers 2001, Claveau et al. 2002). At the whole-tree level, decreases in LAR with increasing tree size followed a similar pattern as observed for FRMR, further suggesting that above- and belowground active tissues become a smaller component of total tree dry mass as a tree increases in height. Both LAR and FRMR declined rapidly until trees were around 1 m tall, a trend already reported for LAR in other species (Claveau et al. 2002). Being small (i.e., less than 1 m in height) in a resource-limited environment may thus be advantageous for survival, because high LAR and FRMR are related to a high light and nutrient capture efficiency per unit of total tissue produced.

Variations in tree species plasticity

Overall, yellow birch had higher physiological plasticity than sugar maple, primarily because of its response to the light environment (Figure 1). Similar light-dependent physiological plasticity has been reported for most shade-intolerant (or pioneer) species (Bazzaz and Carlson 1982, Canham 1988, Valladares et al. 2002). As proposed by Valladares et al. (2002), rapid acclimation of photosynthesis is critical for the efficient use of varying irradiance, and leads to increased carbon gain, thereby facilitating increased growth rates and competitive ability. However, we found that the wide and deep crown of yellow birch showed no significant plasticity during development, whereas the monolayer, umbrella-shaped crown (Waring 1987) of sugar maple showed significant plasticity (Figure 4A). Thus, in low light, the monolayer crown of small sugar maples is likely to be more efficient than the multi-layer

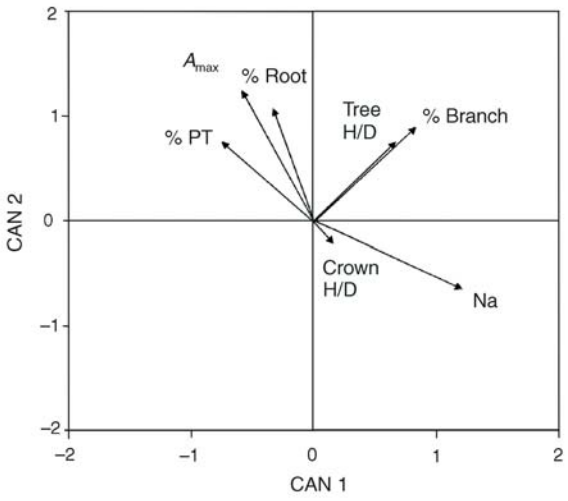

Figure 6. Graphical representation of the vector of the seven parameters driving individual discrimination in the canonical discriminant analysis. Vectors are represented among the two main axes that cumulatively accounted for 90% of the variation. Abbreviations: N_a = leaf nitrogen concentration per area; A_{max} = leaf maximal CO_2 assimilation; Tree H/D = tree height to tree diameter ratio; Crown H/D = crown height to crown diameter ratio; and %PT, %Root and %Branch = leaf, root and branch % of total tree dry mass, respectively.

Table 4. Summary of *P* values for significantly different ($\alpha = 5\%$) distances between the mean of two groups in the canonical discriminant analysis based on the Mahalanobis parameter. Abbrevitions: artificial shade treatment (Sh); unshaded treatment (USh); tall individuals (T); short individuals (S); yellow birch (B); and sugar maple (M).

Group	ShTB	UShTB	ShTM	UShTM	ShSB	UShSB	ShSM	UShSM
ShTB	1	0.0050	0.0141	0.0005	< 0.0001	0.0019	< 0.0001	< 0.0001
UShTB	–	1	0.0002	< 0.0001	< 0.0001	0.0013	< 0.0001	< 0.0001
ShTM	–	–	1	0.8376	< 0.0001	0.0004	< 0.0001	< 0.0001
UShTM	–	–	–	1	< 0.0001	0.0029	< 0.0001	< 0.0001
ShSB	–	–	–	–	1	0.0086	0.0017	< 0.0001
UShSB	–	–	–	–	–	1	< 0.0001	< 0.0001
ShSM	–	–	–	–	–	–	1	0.0439
UShSM	–	–	–	–	–	–	–	1

crown of yellow birch. In addition, small sugar maple tends to allocate less of its total biomass to branches and more to roots compared with yellow birch (Table 3). Kobe (1997) linked this preferential allocation to roots to enhanced survival in low light, because the increased allocation of reserves to storage organs provides a resource buffer that supports the survival of existing tissues or the production of new tissues during periods of net carbon loss. These specific combinations of traits fit well with the greater competitive ability of yellow birch in gaps and the greater overall shade tolerance of sugar maple (Beaudet and Messier 1998, Ricard et al. 2003).

However, the physiological, morphological and allocational differences between yellow birch and sugar maple did not hold constant along both light and size gradients. Most physiological differences between species decreased with decreasing light availability (e.g., g_{smax}, A_{max}, N_a, Table 3), whereas morphological and allocational differences decreased with increasing tree size (e.g., %Crown, Crown H/D, Branches per unit of crown length and %Root, %Branch, Table 3). As Meinzer (2003) suggested, there may be a limited number of physiological processes that can adapt to a stressful environment. This may explain the convergence of leaf physiological traits between our study species in low light regimes. Likewise, a decrease in morphological and allocational differences between species with increasing plant size may be related to the mechanical and physical constraints imposed on larger trees (King 1986, Niklas 1992). Supporting a horizontal crown at 6 m involves totally different constraints and thus carbon costs compared with supporting a horizontal crown at 0.5 m, which is less affected by wind and its own mass.

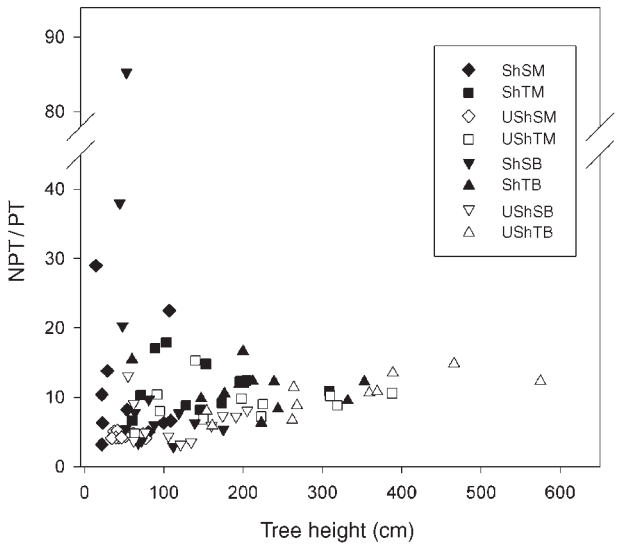

Figure 7. Effects of tree height and artificial shade on non-photosynthetic tissues to photosynthetic tissues ratio (NPT/PT) in sugar maple (M) and yellow birch (B) trees in the Duchesnay forest station, Québec, Canada. Abbreviations: T = tall individuals; S = small individuals; Sh = shaded treatment (solid symbols); and USh = unshaded treatment (open symbols).

Effect of artificial shading

Based on canonical discriminant analysis, we found a clear separation between our study species and between tree size groups in response to shading. Imposition of 50% shade affected the crown morphology of yellow birch more than that of sugar maple. The lower branches of yellow birch died in response to the sudden reduction in light, presumably because they were unable to maintain a positive carbon balance (Sprugel et al. 1991). In contrast, the crown organization of sugar maple was much less affected by the shading treatment (i.e., there was no reduction in crown size, and crown length even increased in smaller seedlings, Figures 5A and 5C). In both species (except taller sugar maple), the shading treatment decreased A_{max} and %PT, but dramatically increased NPT/PT, especially in yellow birch and smaller seedlings. Thus, we suggest that sugar maple was less affected by artificial shading than yellow birch (Table 4, Figure 5) because of its slow growth, flat crown shape when small and high allocation to roots (and thus higher carbon reserves) (C. Gaucher, Université du Québec à Montréal, unpublished data).

Smaller trees of both species were more affected by shading (i.e., they had fewer leaves, yellow leaves and dead branches) than taller plants (Figure 5). Because we found that tree morphological plasticity and LAR decreased with increasing tree size (cf. Messier and Nikinmaa 2000), we expected taller trees to be more affected by a sudden increase in shade than smaller trees. However, in response to the imposed shade treatment,

smaller seedlings increased their NPT/PT ratio to high values compared with unshaded seedlings of the same size (Figure 7). Thus, even if short seedlings have a higher LAR and a greater ability to modify their crown morphology than larger trees, they may not have the necessary reserves to adjust to a sharp reduction in light availability. Larger trees, on the other hand, were able to use their accumulated reserves to survive the sudden reduction in light, at least for the duration of the 4-year study. We hypothesize that the greater morphological plasticity and higher LAR found in shorter seedlings allows them to survive in a stable low-light environment, whereas the larger reserve pool of taller trees allows them to survive for several years following a drastic reduction in light availability.

Conclusions

Based on our findings, it appears that our understanding of the complex combination of traits that explain differences in species functional ecology at the seedling stage cannot be extrapolated to later growth stages. Increasing tree size seems to decrease several inter-specific differences in crown morphology and biomass partitioning, probably because of the increasing pressure imposed by physical and mechanical constraints associated with tree size. Thus, only small seedlings seem able to express fully those specific morphological and allocational traits that confer shade tolerance or gap-use efficiency. Our study also highlights the advantage of being small in a deeply shaded environment (Messier et al. 1999). Nevertheless, the high morphological plasticity of smaller seedlings may not allow them to survive long after a sudden and sustained reduction in light; however, taller trees may be able to survive such an event because of their ability to store reserves in perennial tissues.

Acknowledgments

Financial support was provided by a grant from the Natural Sciences and Engineering Research Council of Canada to C.M. and M.J.L. We gratefully acknowledge numerous field assistants (11) who helped us to dig out trees and especially Joel G. Coburn and Melanie Aubry for discussions and support. We also thank François Lorenzetti and Alain Leduc for advice on statistical analysis and Marilou Beaudet for reviewing this manuscript.

References

Amthor, J.S. 1986. Evolution and applicability of a whole plant respiration model. J. Theor. Biol. 122:473–490.

Baker, F.S. 1949. A revised tolerance table. J. For. 47:179–181.

Bazzaz, F.A. and R.W. Carlson. 1982. Photosynthetic acclimation to variability in the light environment of early and late successional plants. Oecologia 54:313–316.

Beaudet, M. and C. Messier. 1998. Growth and morphological responses of yellow birch, sugar maple and beech seedlings growing under a natural light gradient. Can. J. For. Res. 28:1007–1015.

Beaudet, M., C. Messier, D.W. Hilbert, E. Lo, Z. Wang and M.J. Lechowicz. 2000. Leaf and plant level carbon gain in yellow birch, sugar maple and American beech seedlings from contrasting forest light environments. Can. J. For. Res. 30:390–404.

Bellefleur, P. and G. LaRocque. 1983*a*. Comparaison de la croissance d'espèces ligneuses en milieu ouvert et sous couvert forestier. Can. J. For. Res. 13:508–513.

Bellefleur, P. and G. LaRocque. 1983*b*. Compétition pour le rayonnement solaire en début de succession secondaire dans une érablière à bouleau jaune et hêtre. Can. J. For. Res. 13:514–521.

Bond, B.J. 2000. Age-related changes in photosynthesis of woody plants. Trends Plant Sci. 5:349–353.

Canham, C.D. 1988. Growth and canopy architecture of shade tolerant trees: response to canopy gaps. Ecology 69:786–795.

Canham, C.D., J.S. Denslow, W.J. Platt, J.R. Runkle, T. Spies and P.S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. 20: 620–631.

Canham, C.D., R.K. Kobe, E.F. Latty and R.L. Chazdon. 1999. Interspecific and intraspecific variation in tree seedling survival: effects of allocation to roots versus carbohydrate reserves. Oecologia 121:1–11.

Ceschia, E. 2001. Environmental effects on spatial and seasonal variations of stem respiration in European beech and Norway spruce. Ph.D. Thesis, Swedish University of Agricultural Science, Uppsala, Sweden, 55 p.

Claveau, Y., C. Messier, P.G. Comeau and K.D. Coates. 2002. Growth and crown morphological responses of boreal conifer seedlings and saplings with contrasting shade tolerance to a gradient of light and height. Can. J. For. Res. 32:458–468.

Erdmann, G.G. 1990. *Betula alleghaniensis* Britton, yellow birch. *In* Silvics of North America: Hardwoods. Vol. 2. E.U. Forest Service, Washington, DC, pp 133–147.

Forcier, L.K. 1975. Reproductive strategies and the co-occurrence of climax tree species. Science 189:808–811.

Gardiner, E.S. and J.D. Hodges. 1998. Growth and biomass distribution of cherrybark oak (*Quercus pagoda* Raf.) seedlings as influenced by light availability. For. Ecol. Manage. 108:127–134

Gendron, F., C. Messier and P.G. Comeau. 1998. Comparison of various methods for estimating the mean growing season percent photosynthetic photon flux density in forest. Agric. For. Meteorol. 91:55–70.

Givnish, T.J. 1988. Adaptation to sun and shade: a whole-plant perspective. Aust. J. Plant Physiol. 15:63–92.

Givnish, T.J. 1995. Plant stems: biochemical adaptation for energy capture and influence on species distribution. *In* Plant Stems: Physiology and Functional Morphology. Ed. B.L. Gartner, Academic Press, San Diego, pp 3–49.

Gleeson, S.K. and D. Tilman. 1992. Plant allocation and the multiple limitation hypothesis. Am. Nat. 139:1322–1343.

Godman, R.M., H.W. Yawney and C.H. Tubbs. 1990. *Acer saccharum* Marsh., sugar maple. *In* Silvics of North America: Hardwoods. Vol. 2. E.U. Forest Service, Washington, DC, pp 78–91.

Jarvis, P.G. 1976. The interpretation of the variation in leaf water potential and stomatal conductance found in canopies in the field. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 273:593–610.

King, D.A. 1986. Tree form, height growth, and susceptibility to wind damage in *Acer saccharum*. Ecology 67:980–990.

Kobe, R.K. 1997. Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship and growth. Oikos 80:226–233.

Le Roux, X., H. Sinoquet and M. Vandame. 1999. Spatial distribution of leaf dry weight per area and leaf nitrogen concentration in relation to local radiation regime within an isolated tree crown. Tree Physiol. 19:181–188.

McClure, J.W., T.D. Lee and W.B. Leak. 2000. Gap capture in northern hardwoods: patterns of establishment and height growth in four species. For. Ecol. Manage. 127:181–189.

McConnaughay, K.D.M. and J.S. Coleman. 1999. Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. Ecology 80:2581–2593.

McDowell, N., H. Barnard, B.J. Bond et al. 2002. The relationship between tree height and leaf area:sapwood area ratio. Oecologia 132:12–20.

Meinzer, F.C. 2003. Functional convergence in plant responses to the environment. Oecologia 134:1–11.

Messier, C. and E. Nikinmaa. 2000. Effect of light availability and sapling size on growth, biomass allocation and crown morphology of understory sugar maple, yellow birch and American beech. Ecoscience 7:345–356.

Messier, C. and P. Puttonen. 1995. Spatial and temporal variation in the light environment of developing Scots pine stands: the basis for a quick and efficient method of characterizing light. Can. J. For. Res. 25:343–354.

Messier, C., R. Doucet, J.-C. Ruel, Y. Claveau, C. Kelly and M.J. Lechowicz. 1999. Functional ecology of advance regeneration in relation to light in boreal forests. Can. J. For. Res. 29:812–823.

Naumburg, E., D.S. Ellsworth and R.W. Pearcy. 2001. Crown carbon gain and elevated [CO_2] responses of understory saplings with differing allometry and architecture. Funct. Ecol. 15:263–273.

Niinemets, Ü., O. Kull and J.D. Tenhunen. 1998. An analysis of light effects on foliar morphology, physiology, and light interception in temperate deciduous woody species of contrasting shade tolerance. Tree Physiol. 18:681–696.

Niklas, K.J. 1992. Plant biomechanics: an engineering approach to plant form and function. The University of Chicago Press, Chicago, 607 p.

Perttunen, J., R. Sievänen and E. Nikinmaa. 1998. LIGNUM: a model combining the structure and the functioning of trees. Ecol. Model. 108:189–198.

Poorter L. and M.J.A. Werger. 1999. Light environment, sapling architecture, and leaf display in six rain forest tree species. Am. J. Bot. 86:1464–1473.

Ricard, J.-P., C. Messier, S. Delagrange and M. Beaudet. 2003. Do understory saplings respond to light and below-ground competition?: a field experiment in a north-eastern American hardwood forest and a literature review. Ann. For. Sci. 60:749–756.

Runkle, J.R. 1982. Pattern of disturbance in some old-growth mesic forest of eastern North America. Ecology 63:1533–1546.

Ryan, M.G., B.J. Bond, B.E. Law, R.M. Hubbard, D. Woodruff, E. Cienciala and J. Kučera. 2000. Transpiration and whole-tree conductance in ponderosa pine trees of different heights. Oecologia 124:553–560.

Sprugel, D.G., T.M. Hinckley and W. Schaap. 1991. The theory and practice of branch autonomy. Annu. Rev. Ecol. Syst. 22:309–334.

Sterck, F.J. and F. Bongers. 2001. Crown development in tropical rain forest trees: patterns with tree height and light availability. J. Ecol. 89:1–13.

Tilman, D. 1988. Mechanisms of competition for nutrients and light. *In* Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, Princeton, NJ, pp 52–97.

Valladares, F., J.M. Chico, I. Aranda, L. Balaguer, P. Dizengremel, E. Manrique and E. Dreyer. 2002. The greater seedling high-light tolerance of *Quercus robur* over *Fagus sylvatica* is linked to greater physiological plasticity. Trees 16:359–403.

Walters, M.B. and P.B. Reich. 1999. Research review. Low-light carbon balance and shade tolerance in seedlings of woody plants: do winter deciduous and broad-leaved evergreen species differ? New Phytol. 143:143–154.

Waring, R.H. 1987. Characteristics of trees predisposed to die. BioScience 37:569–574.

Woods, K.D. 2000. Dynamics in late-successional hemlock–hardwood forests over three decades. Ecology 81:110–126.